

# First record of *Saurichthys* (Actinopterygii: Saurichthyidae) from the Late Triassic of eastern Paleo-Tethys

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**Abstract** The saurichthyiform fishes, characterized by a pointed rostrum and a streamlined long and slender body plan, ranked among the top predators of the ichthyofauna in the Early Mesozoic oceanic ecosystem. In a cosmopolitan pattern, these fishes rapidly radiated after the end-Permian mass extinction (EPME) and diversified morphologically and ecologically during the Middle Triassic. Thereafter, they seemingly showed a notable shrinkage from a global distribution to an occurrence basically restricted to the western Paleo-Tethys realm since the Late Triassic. Specifically, there is no saurichthyiform fossil record so far from the marine Late Triassic of South China (eastern Paleo-Tethys), where contrastingly they were highly diversified in stratigraphically older Lagerstätten (Middle Triassic Panxian-Luoping and Xingyi biotas). Here we report the discovery of *Saurichthys taotie* sp. nov. from the Guanling biota of Guizhou and Yunnan provinces, southwestern China. This new species is a medium-sized *Saurichthys* featured by subtriangular subopercles ornamented with densely arranged vertical striae, faint ornamentation on the posterior part of the skull roof, and strong longitudinal ridges decorating the anterodorsal surface of the rostrum. By marking its own group's first occurrence in the Late Triassic of eastern Paleo-Tethyan province, *Saurichthys taotie* suggests that the saurichthyiform fishes were actually much more widespread than previously thought during that geological stage when they showed a considerable decline in the diversity. By still possessing some features previously only seen in its Early Triassic congeners elsewhere, *Saurichthys taotie* sheds new light on the evolutionary and paleobiogeographical history of saurichthyiform fishes.

**Key words** Guanling biota, Guizhou, Yunnan, eastern Paleo-Tethys, Late Triassic, *Saurichthys*

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## 1 Introduction

The end-Permian mass extinction (EPME) profoundly impacted Earth's ecosystem (Chen and Benton, 2012; Benton et al., 2013; Benton and Wu, 2022). Osteichthyes (bony fishes) experienced rapid diversification in the aftermath of this crisis and replaced Chondrichthyes to dominate the ichthyofaunas thereafter (Romano et al., 2016). The Saurichthyiformes (Osteichthyes: Actinopterygii), the earliest 'pike-like predators' among actinopterygian fishes known so far (Kogan et al., 2015, 2020; Tintori, 2019; Benton and Wu, 2022), is a group of specialized Mesozoic fishes with a tapered rostrum, a slender body, and symmetrically positioned median fins (Stensiö, 1925; Rieppel, 1985). This group originated in the Late Permian, radiated in the Early and Middle Triassic, and finally died out in the Middle Jurassic (Liu and Wei, 1988; Mutter et al., 2008; Romano et al., 2012; Maxwell, 2016). During the Early and Middle Triassic, the saurichthyiform fishes exhibited global distribution and invaded both marine and freshwater environments (Romano et al., 2012). They also developed diverse swimming and feeding strategies during this period (Wu et al., 2009, 2011, 2013, 2015, 2018; Kogan et al., 2015). When it came to the Late Triassic, the diversity of these fishes was significantly reduced, and their distribution was basically restricted to the western Paleo-Tethys (Romano et al., 2012). Although *Saurichthys huanshenensis* was reportedly assigned to the age of the Late Triassic of the non-marine Ordos Basin of North China (Chou and Liu, 1957), its age remains controversial (Ge et al., 2007; Chang et al., 2012; personal communications to Liu Jun of IVPP).

The South China basin of the eastern Paleo-Tethyan province documents continuous rock sequences from the Middle Permian to the Upper Triassic with various sedimentary settings (Tong et al., 2019). In the western part of this basin, four exceptional fossil Lagerstätten have been excavated from the border area between Yunnan and Guizhou Provinces: the Anisian Luoping and Panxian biotas, the Ladinian Xingyi biota, and the Carnian Guanling biota (Wang et al., 2008; Jiang et al., 2009; Benton et al., 2013). Abundant well-preserved marine fishes and reptiles have been reported and greatly expanded our knowledge of the recovery of the marine ecosystem after the EPME and the paleobiogeographical history of relevant aquatic vertebrates (Chen and Benton, 2012; Benton et al., 2013; Benton and Wu, 2022). From those fossil Lagerstätten, increasing evidences suggest that the saurichthyiform fishes, ranking among the top predators in local fossil communities, had successfully evolved during the Middle Triassic of South China. In the past decade, one new family, two new genera, and eight new species of Saurichthyiformes from the Middle Triassic Luoping and Panxian biotas have been established (Wu et al., 2009, 2011, 2013, 2015, 2018; Zhang et al., 2010). The younger Xingyi biota has yielded many undescribed saurichthyid specimens that show a notable taxonomic diversity (Jin, 2006 and personal observations). However, saurichthyiform fishes have not yet been reported in either the Guanling biota or the Upper Triassic of the entire eastern Paleo-Tethys (Liu et al., 2006; Romano et al., 2012; Benton et al., 2013; Wu et al., 2018). 'This absence of evidence' was proposed to echo the restricted paleogeographic distribution of this group at that time (Romano et al., 2012). Here we report a new species of *Saurichthys* from the Guanling biota (Xiaowa

Formation, Carnian) as the first record of this group in the Upper Triassic of the eastern Paleo-Tethys. This discovery brings new knowledge of the faunal composition of the Guanling biota and inspires us to reevaluate the paleobiogeographical history of the saurichthyiform fishes during the Late Triassic when they were reportedly losing their diversity.

## 2 Materials and methods

The studied material, curated in the Institute of Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP), includes two specimens. The holotype specimen IVPP V31228 is a dorso-laterally compressed skull preserved with ammonoid *Trachyceras* sp. and bivalves (e.g., *Halobia rugosoides*) in dark grey laminated marlstone. It was excavated from an undescribed outcrop in Longbozi (means Dragon's neck in Chinese) Village, Fuyuan County, Qujing City, Yunnan Province, China (Fig. 1A), about 1 km north of Jiyangshan Village. Due to the coverage of the farmland, the stratum is exposed with only ca. 1.5 m thickness, consisting of thin- to medium-bedded grey to black laminated marlstone with some intercalations of black shale with abundant ammonoids and bivalves (Fig. 1B–D). Several specimens of the ammonoid *Trachyceras multituberculatum* were unearthed during our fieldwork there (Fig. 1E, F), which indicate that the fossiliferous layers belong to the Lower Member of the Xiaowa Formation (formerly called the Wayao Member of Falang Formation) and have an age of late early Carnian, Late Triassic (Xu et al., 2003; Sun et al., 2016). Large pseudoplanktonic crinoids, the iconic creatures of the Guanling biota (Wang et al., 2008), have also been found in the fossil-bearing stratum.

The paratype specimen IVPP V31229 includes a dorso-laterally compressed skull and some anterior vertebral bones of the same individual preserved in laminated yellowish-grey marl with *Trachyceras* sp. and bivalves. It was collected from the Lower Member of the Xiaowa Formation at Xinpu Town, Guanling County, Anshun City, Guizhou Province, which is a well-studied locality of the Guanling biota (Wang et al., 2008). The skull is slightly larger than the holotype and had been severely weathered, which may increase the color and texture contrast between the bones and the matrix (Li et al., 2013). Although the ornamentation on the external surface of the bones has been eroded, the bone sutures and sensory canals can be clearly observed. These two individuals are assigned to one species based on their shared features of the subopercle and the rostrum.

The fossils were mechanically prepared with sharp needles. Photographs were taken under a Nikon SMZ1500 binocular and DJI drone, and the line drawings were done based on a sketched line drawing. For better contrast, the holotype specimen (IVPP V31228) and specimens of *Trachyceras multituberculatum* were dusted with ammonium chloride before being photographed. The rostrum of the holotype specimen was scanned by a micro-computed laminography system (CL) with a beam energy of 150 kV and a flux of 50  $\mu$ A at a resolution of 12.93  $\mu$ m per pixel in the Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences. The measurement conventions (Fig. 2) followed Wu et al.

(2015). As the dorsolateral compression hampers the accurate restoration of the skull depth, the estimated skull depth is measured by the distance from the posteroventral edge of the lower jaw to the midpoint of the width of the dermopterotic covering the cheek bones. The anatomical terminology used in this paper follows Stensiö (1925), Rieppel (1985) and Argýriou et al. (2018).

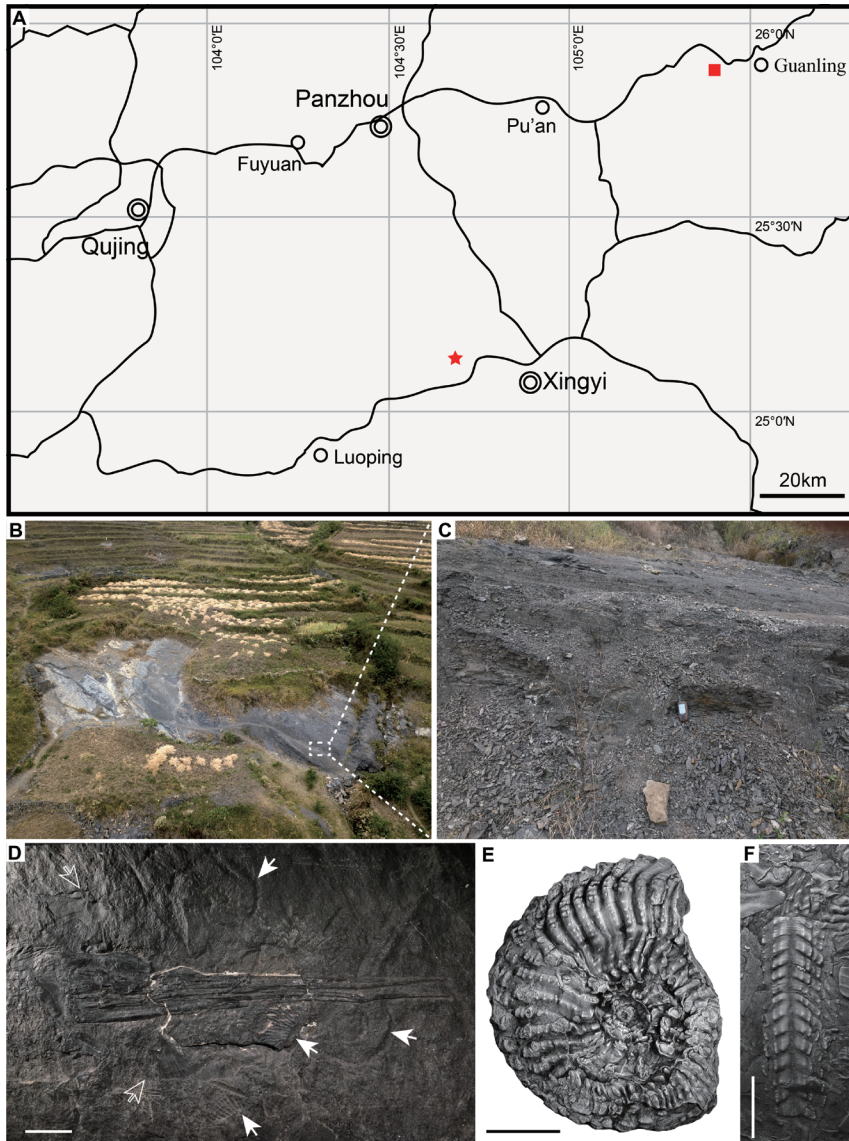


Fig. 1 Geographic sketch map of the studied fossil localities; photographs of the Longbozi Outcrop, and coexisting fossils

A. sketched location map, red pentagram: Longbozi outcrop (Longbozi Village), Fuyun County, Qujing City, Yunnan Province; red square: Xinpu Town, Guizhou Province; B, C. aerial photo (B) and fossiliferous layers (C) of the Longbozi outcrop, GPS in the center of the image is 15 cm long; D–F. photographs of co-occurring fossils from the Longbozi outcrop: D. IVPP V31228, hollow arrows indicate bivalves (*Halobia* sp.), and white arrows indicate *Trachyceras* sp., scale bar = 20 mm; E, F. *Trachyceras multituberculatum* collected from Longbozi outgroup, in lateral (E) and ventral (F) views, scale bars = 5 mm

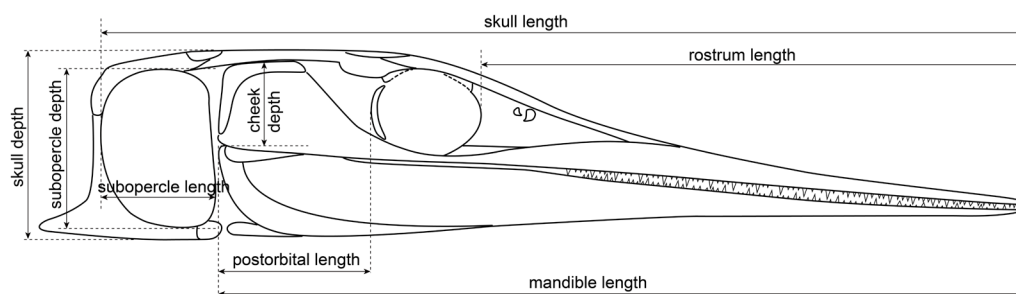


Fig 2 Measurement conventions in current study

### 3 Systematic paleontology

#### Subclass Actinopterygii Cope, 1887

#### Order Saurichthyiformes Aldinger, 1937

#### Family Saurichthyidae sensu Stensiö, 1925

#### Genus *Saurichthys* Agassiz, 1834

#### *Saurichthys taotie* sp. nov.

**Etymology** *taotie*, Taotie (‘饕餮’ in Chinese Pinyin) is a gluttonous monster in ancient Chinese legends, whose head was often engraved on ancient bronzes as decoration. The specific epithet is derived from ‘TaoTie Fish’, a fictional ferocious fish from Chinese science fiction novel series *The Three-Body Problem* by Liu Cixin, as a metaphor for survival competition in the story (Liu, 2010).

**Holotype** IVPP V31228, a dorso-laterally compressed skull preserved with the imprint of the right subopercle and the disarticulated left subopercle (Fig. 3A–D) (for the updated terminology of the opercular apparatus of saurichthyid fishes see Argyriou et al., 2018).

**Paratype** IVPP V31229, a dorso-laterally compressed skull preserved with the disarticulated right subopercle and a series of articulated neural arches of the anterior abdominal region (Fig. 3E–G).

**Type locality** Longbozi outcrop (Village) (N25°7'3", E104°41'29"), Fuyuan County, Qujing City, Yunnan Province, China (Fig. 1A, B, C).

**Horizon** Lower Member of Xiaowa Formation, within *Trachyceras multituberculatum* ammonoid zone, Julian substage, Carnian stage, Upper Triassic.

**Diagnosis** A medium-sized *Saurichthys* with a notably prolonged rostrum (rostrum/mandible length ratio > 0.71); subtriangular subopercle with distinct ornamentation of vertical striae; posterior skull roof decorated with faint ornamentation and the anterodorsal surface of the rostromaxilla with strong longitudinal ridges.

### 4 Description

**General morphology** *Saurichthys taotie* sp. nov. is a medium-sized saurichthyid fish



(for size classes see Tintori, 2013) (Fig. 3) which shows the typical tapering and pointed snout, high postorbital maxillary plate in the cheek region, and a large gill cover bone (subopercle). Based on the length of the skull, the standard body length is estimated to be no less than 600 mm (the minimum estimate is based on a skull/standard body length ratio of *Saurichthys striolatus* which has a fairly long skull (Griffith, 1977; Kogan et al., 2020)). The rostrum occupies 71.5%–76.1% of the mandible length (Table 1). For other measurements of the skull see Table 1.

**Snout** The anteriorly tapered snout of the studied specimens is depressed dorsoventrally so that the dorsal part of its constituting bones can be clearly observed (Fig. 3). The paired rostromaxillae occupy most of the upper jaw. They are fused along the midline and are separated by the frontals posteriorly. The triangular nasaloantorbital on each side has a pointed anterior tip that wedges between the anterior end of the frontal and the posterior part of the rostromaxillae. It contains the openings of two external nares (en.1, 2) with the supraorbital sensory canal passing between them, of which the anterior one is larger than the posterior one. The anteriormost part of the rostromaxillae is decorated with conspicuous longitudinal ridges (Fig. 3A, C). More posteriorly, these ridges are replaced by small tubercles which continue posteriorly and transform into stout vertical striae that cover the lateral surface of the snout. Although the nasaloantorbital is badly damaged in IVPP V31228 and weathered in V31229, some tubercles could be observed on the residual surface of its anterior end.

**Dermal skull roof** Several bone sutures on the dermal skull roof were recognized in the studied specimens (Fig. 3A, B, E). An oval parietal is enclosed by the paired frontals anteriorly and dermopterotics posterolaterally. The frontals extend and narrow anteriorly, but their anteromedial boundaries cannot be recognized in the current material. The paired supraorbital sensory canals are discerned as two parallel dotted lines embedded in grooves that flank the midline suture of the frontals. The dermopterotic is of an irregular trapezoid shape and meets its counterpart along a relatively short and straight suture behind the parietal. The anterior and posterior edges of the dermopterotic are slightly concave to accommodate the parietal and

Table 1 Meristic characters of *Saurichthys taotie* sp. nov.

		IVPP V31228	IVPP V31229
Measurement (mm)	Skull length ( $L_{sk}$ )	181.5	~247.7
	Mandible length ( $L_{mand}$ )	163.0	220.4
	Skull depth ( $D_{sk}$ )	~24	~35
	Rostrum length ( $L_{ro}$ )	~124	~157.5
	Postorbital length ( $L_{po}$ )	~26	~37
	Cheek depth ( $D_{ch}$ )	~12	~18
	Subopercle length ( $L_{sop}$ )	18.5	~27
	Subopercle depth ( $D_{sop}$ )	19.1	~29
Proportion (%)	$L_{ro}/L_{mand}$	76.1	71.5
	$L_{po}/L_{mand}$	15.95	16.8
	$L_{po}/L_{ro}$	21.0	23.5
	$D_{sk}/L_{sk}$	13.2	14.1
	$D_{ch}/L_{po}$	46.1	48.6
	$L_{sop}/D_{sop}$	96.9	93.1

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extrascapulars (not preserved in current material), respectively. The infraorbital sensory canal bends in the flared anterolateral corner of the dermopterotic before it enters the dorsal side of

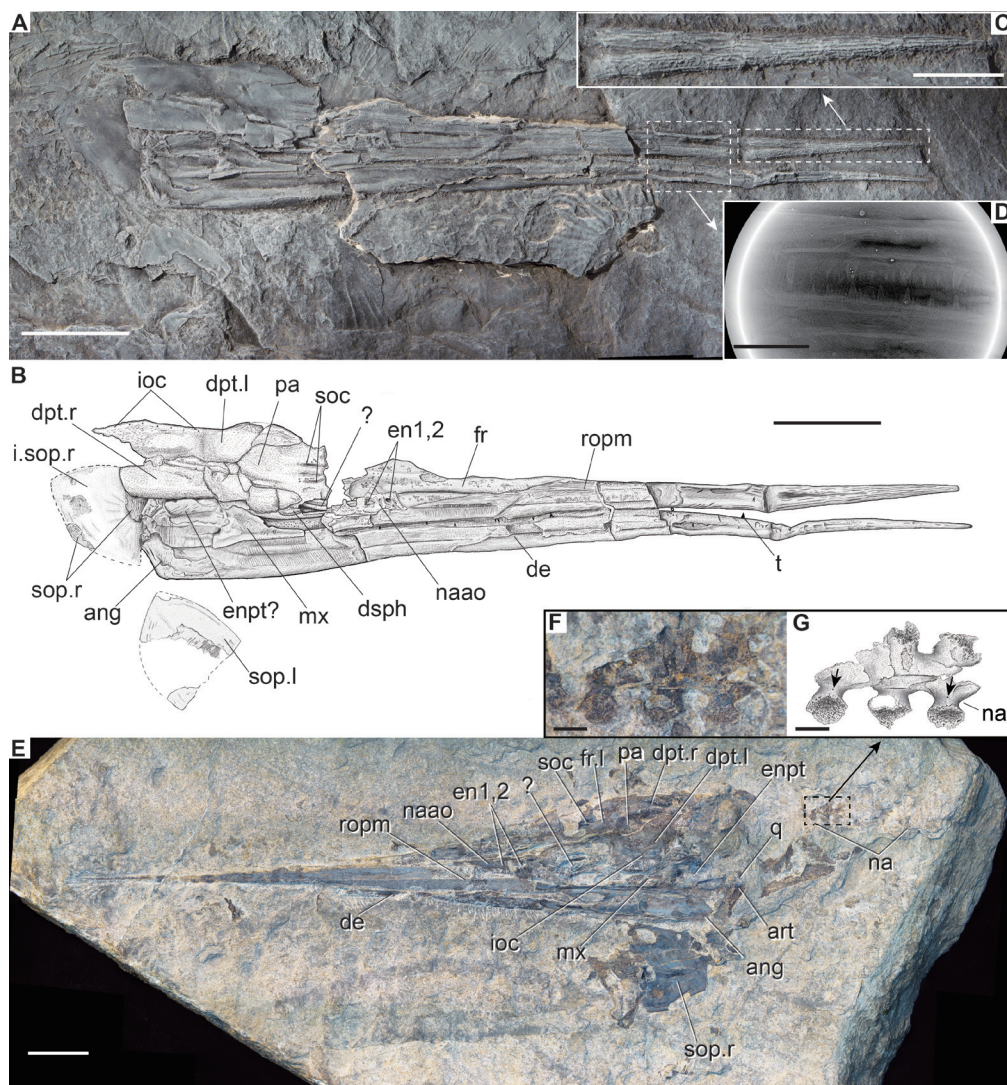


Fig. 3 *Saurichthys taotie* sp. nov. from the Guanling biota (Late Triassic), eastern Paleo-Tethys  
A, B. photograph (A) and line drawing (B) of the holotype IVPP V31228; C. the close-up of the anterior length of the rostrum in A; D. the CL image of a length of the rostrum and the teeth covered by the matrix in A; E. photograph of the paratype IVPP V31229; F, G. close-up image (F) and line drawing (G) of the neural arches preserved in E, black arrows point the foramina in the inner side of the neural arches, which are possibly associated with the spinal nerves or vessels (Wu et al., 2009; 2011; 2015)

Scale bars equal 20 mm in A, B and E, 5 mm in C and D, and 2 mm in F and G

Anatomical abbreviations: ang. angular; art. articular; de. dentary; dpt. l. left dermopterotic; dpt. r. right dermopterotic; dsph. dermosphenotic; en1,2. anterior and posterior external nares; enpt. entopterygoid; fr.l. left frontal; i.sop.r. the imprint of the right subopercle; ioc. infraorbital sensory canal; mx. maxilla; na. neural arch; naao. nasaloantorbital; pa. parietal; q. quadrate; rom. rostromaxilla; soc. supraorbital sensory canal; sop.l. left subopercle; sop.r. right subopercle; t. a tooth; ?. unidentified structure

the latter. More posteriorly, it runs along the lateral margin of the dermopterotic and leaves at the pointed lateral tip of the bone. Some small tubercles are seen on the anterior half of the frontals, whereas the ornamentation is much fainter on the parietal and the dermopterotics, where short and shallow pits and grooves are developed.

**Cheek bones** The cleaver-shaped maxilla greatly narrows below the orbit and extends anteriorly at least to the level of the anterior rim of the orbit (Fig. 3A, B, E). It fairly expands in the postorbital region, occupying the largest part of the cheek. The preopercles were badly damaged in current material so that their suture with the maxilla cannot be clearly restored. An unornamented bony plate is preserved in the position of the damaged preopercle, which is tentatively assigned as the exposed part of the entopterygoid. The ventral ankle of the endochondral quadrate is preserved in the state of articulation with the articular of the lower jaw in IVPP V31229, but the rest part of this bone was weathered away. The maxilla is decorated with fine vertical striae in the postorbital part and faint pits in the suborbital part.

**Lower jaw** The lower jaw protrudes forward; however, it cannot be determined whether it is strictly as long as the upper jaw according to current materials. The dentary is the largest dermal bone of the low jaw that covers the anterior and most of the lateral external surface of the mandible. Like the rostromaxilla, the dentary also tapers anteriorly to form a beak-like bone. At the rear, in a posterodorsally slanted line, the dentary sutures with the angular, which occupies the posteroventral corner of the mandible. The angular takes the shape of an obtuse triangle and extends forward to the level of the posterior rim of the orbit. The surangular cannot be discerned due to the coverage of the displaced maxilla. The articular is observed in V31229 where the posterior part of the angular was not preserved. It is a triangular bone situated at the posterodorsal corner of the mandible and bears the glenoid fossa that receives the ankle of the quadrate. The dentary is decorated with posteriorly inclined striae in the posterior part, whereas the anterior 1/3 length of this bone is ornamented with some short longitudinal ridges, just like those on the corresponding length of the upper jaw. The angular bears a cluster of striae that radiate from its posteroventral corner. No details of the mandibular sensory canal can be detected in the current material.

**Opercular apparatus** The subopercle is an iconic bone lying behind the jaw joint (Fig. 3A, B). *Saurichthys taotie* sp. nov. has a subtriangular subopercle whose length-depth ratio is ca. 1 (Table 1). According to the imprint, the vertical anterior margin of this bone bears a small projection roughly at the midpoint. The posteroventral margin of the subopercle is much more convex than the dorsal margin (Fig. 4A). The internal surface bears some radiating grooves at the anterior part and several concentric wrinkles paralleling the dorsal and posteroventral margins (Fig. 4B). Similar wrinkles were interpreted as growth marks (Griffith, 1959; Rieppel, 1985), which were later challenged by histological evidence (Scheyer et al., 2014). Although all subopercles in the studied material show their medial view or imprint of the internal surface, conspicuous vertical striae are observed from the breach of this bone in the holotype (Fig. 4A).



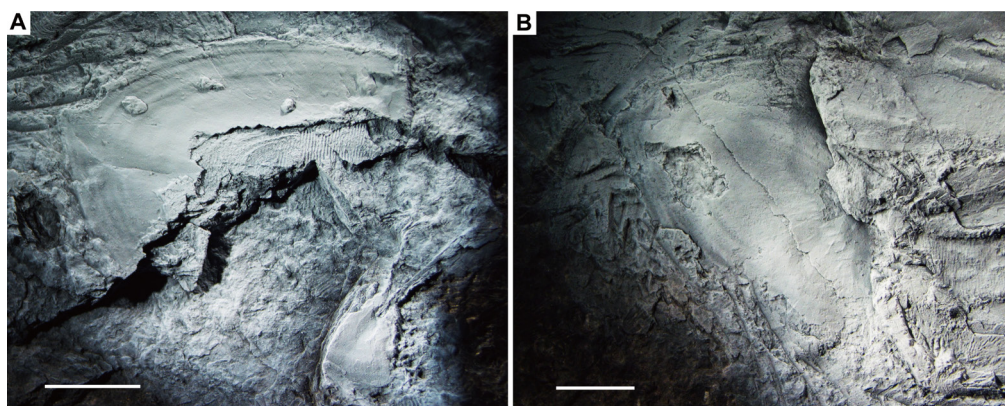


Fig. 4 Photographs of the subopercles of *Saurichthys taotie* sp. nov. (IVPP V31228) from the Guanling biota (Late Triassic), eastern Paleo-Tethys

A. left subopercle; B. imprint and remaining parts of the right subopercle. Scale bars = 5 mm

**Dentition** Only some disarticulated or broken teeth can be directly observed in IVPP V31228. We used CL scanning to detect the dentition *in situ* of the jaws (Fig. 3D). The teeth are conical in shape and can be divided into two size categories. The larger ones, about 2 mm in height in the scanned area, are arranged at regular intervals filled by several smaller teeth (less than 1 mm in height). No “Inzisivlücken” (teeth crypts) along the labial edges is developed. All the exposed teeth are not well preserved and nothing can be said about the arrangement of the ornamentation and the relative height of the enamel cap of the teeth.

**Axial skeleton** Several articulated neural arches are preserved to show their ventral and medial sides in IVPP V31229 (Fig. 3E–G). The exposed part of the neural arch is roughly ‘T’-shaped, with its vertical axis stout and anterior and posterior edges constricted below the level of the pre- and postzygapophysis. On the medial surface, at least one small foramen is detected for which the analogues are present in every other neural arch in other saurichthyid fishes (Wu et al., 2009, 2011, 2015; Maxwell et al., 2016). The sucker-like ventral part with a rough texture is the ‘base’ of the neural arch that was originally attached to the notochord *in vivo*.

## 5 Discussion

### 5.1 Comparison

As the morphological information of the new species is mostly from the skull and the gill cover, the comparison is confined to its congeners and more broadly to other saurichthyiform fishes whose cranial and opercular features are well-known. During the Triassic, the South China (eastern Paleo-Tethys) was an evolutionary hotspot of the saurichthyiform fishes (Wu et al., 2009, 2011, 2013, 2015, 2018; Zhang et al., 2010; Benton and Wu, 2022). Those species from the Anisian (Middle Triassic) of Yunnan and Guizhou Provinces of China can be easily distinguished from *Saurichthys taotie* sp. nov. in the cranial morphology. The most distinct feature of the new species is the shape of the subopercle. The subopercle in the new species

is subtriangular in shape, whereas in all named saurichthyiform fishes from the Luoping and the Panxian biotas it is generally elliptical in shape and usually deeper than long (Fig. 5). *Yelangichthys macrocephalus*, excavated from the Panxian biota, constitutes the monotypic Yelangichthyidae, the sister group of Saurichthyidae (Wu et al., 2013; Argyriou et al., 2018; Ren and Xu, 2021). It departs from *Saurichthys taotie* sp. nov. in having small screwdriver-like teeth, a roughly long-oval subopercle, and the strong and tubercular ornamentation on the dermal skull roof (Wu et al., 2013). According to the observations on our large collection of undescribed material of *Saurichthys* from the Ladinian Xingyi biota, none of them exhibits a similar subopercle (Fig. 5G).

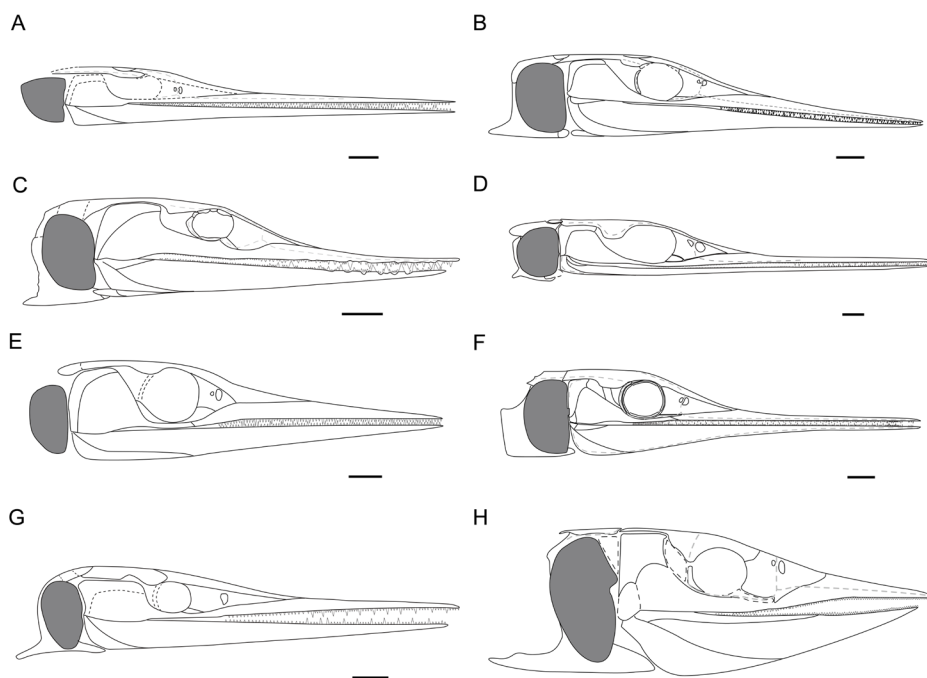


Fig. 5 Comparison of the skulls of some known saurichthyiform fishes from the Middle to Late Triassic of Yunnan and Guizhou, China

A. *Saurichthys taotie* sp. nov.; B. *S. dawaziensis* (Wu et al., 2009); C. *S. yangjuanensis* (Wu et al., 2015); D. *S. spinosa* (Wu et al., 2018); E. *S. yunnanensis* (Zhang et al., 2010); F. *Sinosaurichthys longipectoralis* (Wu et al., 2011); G. *Saurichthys* sp. from the Ladinian Xingyi biota, southwestern Guizhou Province (personal observations); H. *Yelangichthys macrocephalus* (Wu et al., 2013)

Gray shadows highlight the subopercles. Scale bars equal 2 mm in D and 10 mm in other illustrations

Apart from the configural differences in the gill cover, the rostrum length and the jaw (tooth) features, as well as the extent of the bony ornamentation of the new species also bear some taxonomic significance. Regarding the forms from the eastern Paleo-Tethyan realm, *Saurichthys dawaziensis* and *S. yangjuanensis* possess relatively shorter rostra but are equipped with larger teeth accommodated in labial crypts and lack longitudinal ridges at the pointed end of the rostromaxilla (Wu et al., 2009, 2015). *Saurichthys yangjuanensis* also

differs from the new species in having stronger ornamentation on the dermal skull roof (Wu et al., 2015). *Saurichthys yunnanensis* differs from the new species in possessing a proportionally shorter rostrum ( $L_{ro}/L_{mand} \approx 65\%$ ) and deeper skull ( $D_{sk}/L_{sk} \approx 25\%$ ) (Zhang et al., 2010). The skull features of *S. spinosa* are more distinctive and this species has a much smaller size, a very narrow interorbital region, and a strongly decorated dermal skull roof (Wu et al., 2018). The *Sinosaurichthys* species exhibit a similarly prolonged rostrum, for example, the rostrum makes up 73%–76% of mandible length in *Sinosaurichthys longipectoralis*. However, this species differs from *S. taotie* sp. nov. in having a deeper skull, proportionally smaller teeth, dense tubercles on the dermal skull roof, and a weakly decorated rostrum tip (Wu et al., 2011).

Among the Late Triassic *Saurichthys* with well-preserved skull and gill cover, three species from the western Paleo-Tethys have been known based on relatively complete skeletons (Romano et al., 2012). *Saurichthys striolatus* resembles the new species in having a prolonged rostrum with a  $L_{ro}/L_{mand}$  ratio of ca. 75% (personal observations of SMNS 96342, curated in the Stuttgart State Museum of Natural History, Germany). However, its body size is much smaller than the new species and possesses a subquadratic subopercle (Griffith, 1959; Kogan et al., 2020). *S. calcaratus* also has a prolonged rostrum and medium body size. Its subopercle is ornamented with dense vertical striae like that of *S. taotie* sp. nov., but this bone is different from that of the latter which is slightly longer than high and has a convex posterior margin. Additionally, in comparison to the size of the postorbital maxilla-preopercular plate and lower jaw, the subopercle of *S. calcaratus* appears to be smaller than that of *S. taotie* sp. nov. (Kogan et al., 2020 and personal communications to Ilja Kogan). In addition, *S. calcaratus* shows a fairly large nasaloantorbital (Griffith, 1977). Distinct from the new species, *S. deperditus* (= *S. “krambergeri”*) has oval-shaped subopercles, larger teeth (3.3–5.2 mm high), and teeth crypts along the labial edge of the jaws (Griffith, 1962).

Distinct from all congeners from other regions of the world (see Wilson et al., 2013; Werneburg et al., 2014; Maxwell et al., 2015, 2016), *S. taotie* sp. nov. shares the subtriangular subopercle with three *Saurichthys* species from the Early Triassic of Madagascar (Kogan and Romano, 2016) and Boreal sea (Stensiö, 1925) and from the Middle to Late Triassic of central Asia (Kogan et al., 2009, 2020), respectively. However, the subopercle of *S. madagascariensis* (late Induan) displays a posteroventrally inclined anterodorsal margin. It is also different from *S. taotie* sp. nov. in having coarse ornamentation on the dermal skull roof and a relatively short rostrum (Kogan and Romano, 2016). *Saurichthys elongatus* more closely resembles the new species in the cranial and subopercular morphology and faint ornamentation on the dermal skull roof, but it is distinct from the new species in the pattern of ornamentation on the subopercle (Stensiö, 1925). *Saurichthys orientalis* from the Middle-Upper Triassic lacustrine deposits in central Asia has a similarly subtriangular subopercle, but the convexity of the dorsal and posteroventral margins and the extension of the anterior border of the subopercle are different from the new species described here (Kogan et al., 2009, 2020).

## 5.2 Paleobiogeographical implications

The absence of saurichthyiform fishes in former fossil records from the Late Triassic of the eastern Paleo-Tethys was regarded as the indicator of the shrinking paleogeographical distribution and declining diversity of these fishes at that stage (Romano et al., 2012). Since then, their distribution seems mainly restricted to the western Paleo-Tethys and Euramerican Realm (Romano et al., 2012). The discovery of *Saurichthys taotie* sp. nov. in the Guanling biota, South China, clearly indicates that some representatives of this fish group still lived in the eastern Paleo-Tethyan region at least by the early Late Triassic (Fig. 6). Moreover, the resultantly updated temporal and spatial distribution of some morphological features of taxonomic significance in *Saurichthys* suggests that their paleobiogeographical process might be more complex than previously thought (Romano et al., 2012). The subopercle (the traditionally termed ‘opercle’, see Argyriou et al., 2018 for definition) shape has been extensively treated as a taxonomic character in *Saurichthys* (Rieppel, 1992; Wilson et al., 2013; Maxwell et al., 2015; Kogan and Romano, 2016; Wu et al., 2018) and is one of the key features distinguishing the basal species, e.g. *S. madagascariensis* from the Early Triassic of Madagascar (Kogan and Romano, 2016) and *S. orientalis* from the Late Triassic of Central

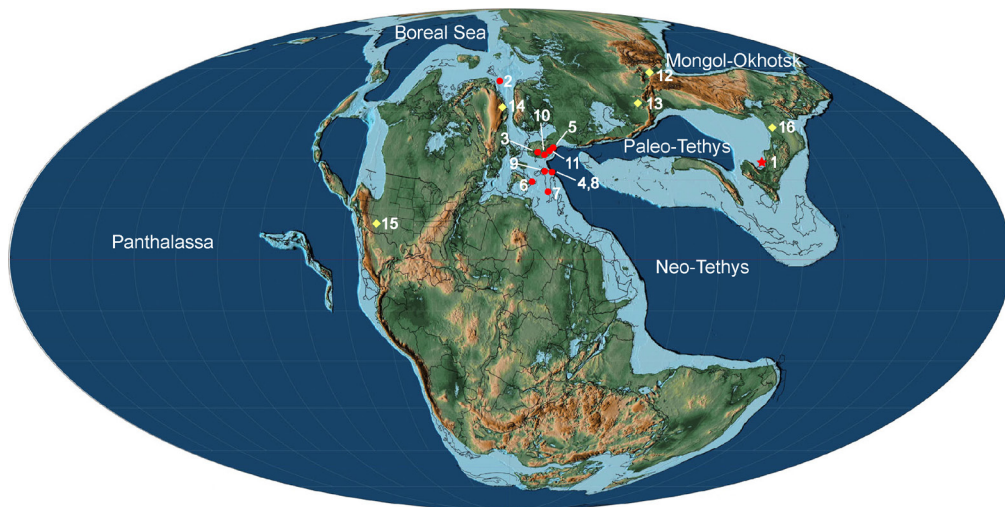


Fig. 6 Paleogeographical distribution of *Saurichthys* in the Late Triassic  
Paleogeographic map adopted from Scotese (2014), records of *Saurichthys* mostly adopted from Romano et al. (2012) with minor modification

Fossil records from the marine deposits (red dots): 1. *Saurichthys taotie* sp. nov., Guizhou and Yunnan Provinces, China; 2. *Saurichthys*? sp., Svalbard, Norway; 3. *S. irregularis*, Württemberg, Germany; 4. *S. striolatus* (Carnian), Friuli-Venezia Giulia, Italy; 5. *S. calcaratus*, Lower Austria, Austria; 6. *S.* sp., Catalonia, Spain; 7. *S. deperditus*, Campania, Italy; 8. *S.* sp. (Norian), Friuli-Venezia Giulia, Italy; 9. *S. deperditus*, *S. seefeldensis*, *S.* sp., Lombardy, Italy; 10. *S. seefeldensis*, Tyrol, Austria; 11. *S. deperditus* (= *S. "krambergeri"*), Upper Austria, Austria; Fossil records from freshwater deposits (yellow diamond): 12. *S.* sp., Junggar Basin, Xinjiang, China (Liu and Wei, 1988); 13. *S. orientalis*, (Kogan et al., 2009); 14. *Saurichthys*? sp., Greenland (Jenkins et al. 1994); 15. *S.* sp., Arizona, USA (Kligman et al., 2017); 16. *S. huanshenensis* (with questionable age), Shaanxi, China (Chou and Liu, 1957)



Asia (Kogan et al., 2009; Maxwell et al., 2015), from other more derived congeners including those from the eastern Paleo-Tethyan region (Wu et al., 2018). Regarding subopercle's general morphology, *Saurichthys taotie* sp. nov. closely resembles the abovementioned basal congeneric species (Kogan et al., 2009; Kogan and Romano, 2016) and *S. elongatus* of the Early Triassic of Spitsbergen (Stensiö, 1925), but notably diverges from all stratigraphically older saurichthyid fishes from the eastern Paleo-Tethys whose subopercles were well-preserved (Liu and Wei, 1988; Wu et al., 2009, 2011, 2013, 2015, 2018; Zhang et al., 2010). In this sense, albeit the unfeasibility of a phylogenetic analysis for the new fish due to the incompleteness of the fossil material, it is tempting to infer that *Saurichthys taotie* sp. nov. might be the derivative from a certain immigrant from elsewhere, taking into account the hypothesized repeated trans-oceanic dispersals among Middle Triassic saurichthyid fishes between eastern and western Paleo-Tethys (Maxwell et al., 2015). Admittedly, such a hypothesis should be tested in a strong phylogenetic framework incorporating sufficient fish taxa and morphological details of the new species. However, this is beyond the scope of this paper given the quality of the data at hand.

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## 晚三叠世东特提斯洋龙鱼属(*Saurichthys*) (*Actinopterygii*: *Saurichthyidae*)的首次记录

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**摘要:** 龙鱼类具尖吻和流线型的细长体型, 是中生代早期海洋鱼群中的顶级捕食者。经历

晚二叠世生物大绝灭(EPME)后, 龙鱼类在全球范围内快速辐射, 并于中三叠世时期在形态特征及适应策略上发展出可观的多样性。先前的化石记录显示, 曾经全球广布的龙鱼类似乎自晚三叠世开始收缩至西特提斯洋。当时海生脊椎动物多样性的热点—东特提斯洋区中国华南晚三叠世海相地层中迄今尚无龙鱼类的记录, 与此呈鲜明对照的是, 该地区更低层位(如中三叠世盘县—罗平生物群和兴义生物群)的数个化石库(Lagerstätten)却保存有高度多样化的龙鱼类化石。报道产自中国西南地区(黔西南和滇东地区)晚三叠世早期的关岭生物群的龙鱼属(*Saurichthys*)—新种——饕餮龙鱼(*Saurichthys taotie* sp. nov. )。饕餮龙鱼体型中等, 其主要特征有: 下鳃盖骨(subopercle)近三角形且外侧具密集纵纹, 颅顶后部纹饰较弱, 吻部前端背缘发育显著的纵嵴。作为龙鱼类在晚三叠世东特提斯洋区的首次记录, 饕餮龙鱼的发现说明当时这一类群的多样性虽然在全球范围内呈现显著的下降, 但它们的地理分布实际上比先前的认识广阔得多。此外, 饕餮龙鱼保留一些此前仅见于早三叠世同类的特征, 为认识龙鱼类的演化和生物地理学历史带来新的思考。

**关键词:** 关岭生物群, 贵州, 云南, 东特提斯洋, 晚三叠世, 龙鱼类

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